A MODERN REVIEW OF THE HISTORY OF THE PINE HAWK-MOTH *SPHINX PINASTRI* L. (LEP.: SPHINGIDAE) IN BRITAIN, WITH A EUROPEAN PERSPECTIVE

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Abstract

The 200 year history and fluctuating territorial status of *Sphinx pinastri* L. in Great Britain is reviewed and investigated. The potential sources of British colonies are explored and the reasons for an increasing range towards the north-east since the 1920s is discussed. A brief comparative perspective on the similar continental record is also presented. It is concluded that immigrant specimens from the continent probably sourced many UK colonies, that natural global warming dictated colonisation, that the expansion was exclusively sourced from Dorset, and that this was a race new to the country which overran a previously long-established strain.

Introduction

Even though several rigorous and admirable reviews and collations have been made of the early British records and history of *Sphinx pinastri*, Newman (1965), rightly considered that "A certain amount of mystery surrounds the Pine Hawk". Almost a hundred years ago, J. W. Tutt (1904) individually listed, and controversially discussed in detail, almost all of the known 19th century records made in our islands and on mainland Europe. In 1929, W. Parkinson Curtis added particulars of the nation's intervening sightings (Curtis, 1930a: 1930b), and then in 1947 a critical re-evaluation of the very earliest reports was made by P. B. M. Allan (Allan, 1947). But aside from a large number of subsequent records individually published in various entomological magazines and county lists, and three modern distribution maps published between 1973 and 1980 (Heath, 1973: Gilchrist, 1979: Heath, 1980), there the matter has effectively rested for more than half a century.

A number of visually-similar pine-feeding *Sphinx* are listed and illustrated in *Hawk Moths of the World*, (D'Abrera, 1986). Of those species occurring in Asia and Europe, *S. oberthueri* R. & J. and *S. caligineus* But. inhabit China, and *S. pinastri* L., *S. morio* R. & J., and *S. maurorum* Jor., Europe. Only *S. pinastri* has been recorded in North America, in parts of the Canadian Rocky Mountains and the eastern U.S.A. Several European subspecies of the Pine Hawk moth have also been proposed (Jordan, 1931: Derzhavets, 1979), but their reality is still subject to divergent opinion (Pittaway, 1993; 2000: Danner, Eitschberger, & Surholt, 1998). So far, only *S. pinastri pinastri* has been detected in Great Britain.

Once called "the Fir-tree Arrow-tail-moth" (Lucas, 1895), the now more simply-named Pine Hawk is currently well distributed in south-east England and much less so as far north as Yorkshire – but this was not always the case. During the last half of the 19th century, after approaching a century of recorded national collecting, this species was generally thought "very rare in Britain" (Humphreys, c.1860: Kirby,

1897: Tutt, 1902), or "a scarce casual only" (Meyrick, 1895). There had been just four districts where this insect was known to occur with any regularity, and even the few recognised sites were surrounded by controversy. The moth was evidently established in Suffolk, and probably sometimes in Dorset and near London. Extraordinarily, there were also around half a dozen early records from Scotland – the very earliest stretching back to the late 18th century – but even now, at the beginning of the 21st century, the species has yet to be recorded from Ireland or Wales.

Biology

The adult insect flies mainly from mid June to mid August, more unusually from late April or into September. It is single-brooded in the Britain – there is no coincidence between late records and hot summers. A few of our late sightings have been made near the south coast, but most are found in sympathetic native habitats which have been long-known to boast local colonies of *pinastri*.

It has been implied that in some counties *pinastri* used to fare better "on the lighter, acid soils", as in Hampshire (Goater, 1974) and on the inherent "heath-fir-birch area of Eastern Dorset" (Curtis, 1930a), but in Sussex the species has always been just as numerous – or even more so – amongst artificial pine plantations. Nowadays, nationwide, *pinastri* usually occurs fairly commonly on surviving ancient semi-natural pine-clad heathland and amongst modern alien coniferous plantations, but singletons are also occasionally found at mercury vapour lights situated in more foreign habitats. In addition to the lure of ultra violet light and nectar – it was learnt earlyon that "the perfect insect is sometimes captured hovering over the honeysuckle in the twilight" (Tutt, 1902) and that it visited tobacco-plant flowers – many specimens have been found at rest on pine tree-trunks. Some searchers made such discoveries just "on the leeward side" of the trees, at heights between five and nine feet (Johnson, 1940) or from "two to twelve feet" (Cockayne, 1926), and "without exception ... by viewing the trees from the south-east" from almost ground level to "rather less than five feet" (Mactaggart, 1922), while others found them "in every aspect" "from about 4 to 14 feet from the ground" (Tutt, 1901-5).

Ova are generally deposited "singly on the needles of the pine in June and July", although "sometimes little groups of from two to a dozen are laid together" (Tutt, 1904). The caterpillar stage generally lasts from about late June to mid September. Modern authorities state that larvae only feed diurnally (Pittaway, 2000) but early breeders reported that they "appear to eat (both) by night and day" (Tutt, 1904). The caterpillar's preferred foodplant is the (mature) needles of Scots Pine *Pinus sylvestris*, although Norway Spruce *Picea abies* (Gilchrist, 1979) and Corsican Pine *Pinus nigra* var. *maritima* (M. M. Betts; Hope Entomological Collections) are sometimes utilised. Further evergreen trees were listed as foodplants during the Victorian era – although some may have only been recorded on the continent – including Maritime Pine *P. pinaster*, Weymouth Pine *P. strobus*, Himalayan Pine *P. wallichiana*, Austrian Pine *P. nigra*, several species of Silver Fir *Abies* spp., European Larch *Larix decidua*, Cedar of Lebanon *Cedrus libani*, and Deodar *C. deodara* (Lucas, 1895: Tutt, 1904), and more recently Douglas Fir *Pseudotsuga menziesii* (Pittaway, 2000). 19th century

breeders discovered that "The first and last moults appear to be the most dangerous periods for larvae" because "feeding them on too green and succulent food... produces diarrhoea and the larvae turn almost to water" (Tutt, 1895: 1904), and 20th century enthusiasts also found that "some broods do fail due to viruses" (Porter, 1997). The species overwinters as a pupa in a shallow subterranean excavation under fallen pine needles or in earth from mid September to around early June (Porter, 1997), this occasionally extending over two seasons (Stokoe & Stovin, 1958).

The early records

So dubious was the Victorian collectors' perception of the awkward earliest boreal records that it was "By many doubted as a British species" (Stainton, 1857), some national authorities dismissing them altogether from otherwise extensive lists of British moths (Morris, 1868: Newman, 1869). however, during the final quarter of the 19th century, with the benefit of hindsight and knowledge of a sudden clutch of subsequent records from the east coast of England, later authors thought that these judgements had been made "on account of the unreasonable incredulity which is too often the fashion to regard all records that have not been reconfirmed during the last few years" (Kirby, 1897). Even today the whole issue of old Scottish *pinastri* is evaded in the leading series of reference books on our national macro-Lepidoptera; again, none of these records are even mentioned (Gilchrist, 1979).

Scotland and Northern England

As early as 1800 there was already a "traditionary report" that Scotland was home to the Pine Hawk (Donovan, 1800). In 1811, the accuracy of this folklore was confirmed, when at least two specimens were collected from Ravelston Wood near Edinburgh (sometimes called Rivelstone or Rivelston Wood) (Stephens, 1828: Westwood, 1849; 1854). The last known of an intermittent series from Ravelston was taken in 1818 (Walker, 1907-9). Then in 1827, possibly 1828, an adult was found in Cumberland, "hanging in the position common to the family when recently escaped from the pupa state, to a portion of the root of a fir-tree..... at the side of a fir plantation on Lattrigg, a low mountain near the foot of Skiddaw" (Marshall, 1842: Walker, 1904). In 1860, a collector's attention was drawn to "a full-fed larva..... crawling down the trunk of a Scotch fir tree" at Achnacroish on the eastern side of the Isle of Mull. An adult was successfully bred out in 1861, while another caterpillar seen in the same locality during this same year died within a week of discovery (Edwards, 1886). No further northern records then came to notice until an adult was taken in a domestic garden at Linthorpe (Middlesbrough) in Yorkshire in 1900 (Lofthouse, 1903) and two more were found at rest near Aberdeen in 1928. One of the Scottish specimens had "just emerged; a portion of the pupa-case still remained on the head". The other example, worn, was found in the same locality three days later (Esson, 1928). It seems extraordinary, especially in view of its later history elsewhere in this country, but the Pine Hawk has never been authoritatively detected to the north of Malton in Yorkshire since that date.

Not surprisingly, interpretations of the Scottish records have differed. Some authorities viewed them with a jaundiced eye from the start. Even by 1836 it was being publicly said by a Scotsman on the spot that the Pine Hawk "certainly was never taken in Ravelston Wood, near Edinburgh" (Duncan, 1836). By 1904, Tutt had become excessively cynical over our national records, rather arrogantly stating that errors were suspected to be "incidental to and inseparable from the attempted study of a scientific subject by a large number of poorly equipped students". He added that "A few (accurately identified records) may be due to 'escapes', but there is much indirect evidence furnished ... pointing to grave doubts as to whether the species ever was sedentary (anywhere) in our Islands" (Tutt, 1904). A few years later L. W. Newman and H. A. Leeds baldly summed up its northern history, observing that the species had been "introduced into Scotland as larvae but (it) soon died out" (Newman & Leeds, 1913) – although they provided neither evidence nor argument – a statement that may well have been a mix-up with its history in Suffolk. Then, during the 1960s , E. B. Ford, one of the nation's leading lepidopterists, believed that "it is possibly less rare than supposed and (is still) a native" in Scotland (Ford, 1967). Nonetheless, as has already been mentioned, the few more modern writers have ignored all early records ever made north of an imaginary line drawn from Boston in Lincolnshire to the River Severn (Gilchrist, 1979).

A recent inquiry about the survival of the habitat at Ravelston Wood to K. Bland of the National Museums of Scotland at Edinburgh threw another complicating but speculative light on the early records. Bland confirmed that Ravelston Wood, at map reference NT2274, "is now incorporated into the suburbs of Edinburgh and is largely lost as a wood. Woodland survived close by on Corstorphin Hill, but it is Oak/Beech (*Quercus/Fagus*) dominated, with only occasional Pines. The fragments of the wood that have survived in Ravelston suggest they are remnants of similar Oak/Beech woodland. I have never felt that the habitat was suitable for *pinastri*". He also suggested that the original locality might have been confused "for Ravelrig Wood which is some 10 miles out of town" near Balerno, and which still "has quite a few old pine stands".

The strange, isolated chronicle of the Pine Hawk so far north sits rather uneasily with much (but not all) of its remaining British history – yet it is impossible to dismiss the records as a collection of frauds, introductions, and errors. The only supporting evidence of similar entomological eccentricity concerns the Black-veined White butterfly *Aporia crataegi* L.. Sightings of this species were reported from Hawick, in Roxburghshire, at some time before 1845, a note considered probably erroneous by many experts, and more certainly at Bishops Wood and Stockton Forest in Yorkshire in around the 1870s (Pratt, 1989). Even more interestingly, in an extraordinary and unique episode for this butterfly in Scotland, "In 1974 stock from a few hundred Spanish ova began to be reared outside in Fife ... The next season saw about 200 butterflies successfully emerge and the following year about 100". Protected from avian predation, "This artificially assisted introduction... continued, with reinforcements from Swiss/Italian border stock in 1978", up until at least 1982 (Pratt,

1983). Subsequent contact with the colony's owner to determine its fate proved fruitless. Still, this provides a precedent which proves that under very specific (and in this case protected) circumstances, a particular lepidopteran can temporarily exist within an island of environmental advantage which allows temporary residency far outside of its normal range – but sooner or later they die out, if conditions are too harsh or the time required for adapting to new conditions is too short (Hengeveld, 1990).

Suffolk

Many entomologists believe that the Pine Hawk has been settled in Suffolk "for centuries, although undiscovered" early on (Newman, 1965). But while the area's records only officially commence in 1872 and 1875, with sightings at Harwich and Woodbridge respectively (Lucas, 1895: Tutt, 1902), the county's published history of *pinastri* could yet stretch back another 40 years, as an unspecified "Sussex" sighting made at some time before 1832 (Rennie, 1832) may well have been an error for Suffolk (Pratt, 1999). Whatever, there is no doubt that the moth was well-established on this part of the east coast during the final quarter of the 19th century, as records were published from a number of different collectors almost annually in the entomological magazines of the day. Furthermore, from 1892 to 1895 inclusive the Pine Hawk was locally common, as a single collector could beat out 100 larvae, dig up pupae, and encounter up to 40 adults during one season's work (Bloomfield, 1890: Mellusson, 1895: Tutt, 1904). Numbers quickly fell back again after that sequence and by 1904 some national authorities even considered the moth extinct in the county (Tutt, 1904). Nonetheless, the insect continued to episodically come to notice in Suffolk throughout the 20th century.

This much of the story of *pinastri* in Suffolk is comparatively straightforward. However, in 1880 or 1881 there does seem to have been an attempt to introduce continental specimens to the district, the circumstances of which have been fully discussed previously (Allan, 1947). Availability would not have been a problem to Victorian enthusiasts, as pupae could "be obtained for a penny or twopence each" (Tutt, 1902), the species being "exceedingly common on the Continent" in pine woods (Tutt, 1904). The easy acquisition of foreign *pinastri* in Britain so affected Tutt's views that in 1904 he declared that "a direct and apparently successful attempt had been made to acclimatise the species in Suffolk, and those of us who possess Suffolk caught and Suffolk bred examples no doubt owe our specimens indirectly to these introductions". He then had "grave doubts as to whether the species ever was sedentary in our Islands", and concluded "from the gradual decadence of the progeny resulting from the Suffolk introductions... (that) there is no real natural tendency for the species to become acclimatised and take up a permanent residence here" (Tutt, 1904). Others more simply described the species as "apparently naturalised in Suffolk" (Meyrick, 1895). However, the foreign specimens were released at least nineyears after the very first discovery of the Pine Hawk in the county, and were therefore almost certainly only additions to an area already boasting at least one feral colony. Moreover, it has been shown that less

than one in a hundred attempts at butterfly introduction in the UK are genuinely successful *(Oates & Warren, 1990)* – that is, become viably self-sustaining without further augmentation for more than 25 years – the main reason for this extremely poor success-rate being that introductions are made with species or races that are positioned outside of their current range of environmental advantage.

Essex

Aside from the border sighting made at Harwich in 1872 (Lucas, 1895), this probably being an outlying record from the adjacent clutch of early Suffolk colonies, the inaugural Essex Pine Hawk was taken at an unspecified locality in 1897 (Booth Museum, coll.). No further early encounters took place until 1956 at Lexden (Colchester) and three years later at Bradwell-on-Sea (Firmin et al, 1975). The more regular recording of *pinastri* in Essex commenced in 1983.

London area

The earliest known London area records were made in about 1800 near Colney Hatch Wood and at Esher (Haworth, 1803: Stephens, 1828). No more specimens were apparently seen by Victorian collectors until 1884 and 1885, when an adult and a larva were noted at West Wickham Wood and near Wimbledon respectively (Tutt, 1904). By 1895, its presence near London was considered "a thing of the past" (Lucas, 1895) – but two years later the moth was taken at Weybridge (Tarbat, 1897). The final report within this particular episodic series concerned the discovery of a pupa at Kew Gardens in 1907 (Lucas, 1907), although another batch of records was to be made during the last half of the 20th century. As in northern Britain, the published early historical record is similar to that of a transitory resident.

South-west England

The earliest known Dorset record was made "among tall pines in the middle of Bournemouth" in about 1885 (Mansfield, 1938). Nothing more was then publicly heard of the species until further adults were noted at Poole in 1908 and at Bridport in 1917 (Curtis, 1930a). By 1929, the insect was fairly common over a large area of eastern Dorset (Curtis, 1930b). This colony was situated in the "trough of Poole", where numbers were just as high in 1931 (King, 1931). Regular sightings have been made in the county ever since. At about that time some national experts considered that the species had "certainly been previously overlooked" in Dorset (de Worms, 1934) and, while the early history is extremely thin, at least in part due to an undoubted neglect of the county by pioneering lepidopterists, there is every reason to believe that the moth has been permanently established in the county since 1908 and probably since at least the late 19th century.

The first Somerset sighting came from Hinton St George in 1853 (often referred to as "Crewkerne") – this probably being a front-line part of the Dorset colony – but no more *pinastri* were to be seen in the county for more than a century. The modern era

opened with a record at Minehead in 1957 (Chappel, 1957), and this was followed by other records at Street at some time between 1982 and 1990, at Chard and Wincanton both in 1992 and 1996, at Langport in 1994 (J. C. Lidgate; pers. comm.), and at Timsbury in 1996 (M. Bailey; pers. comm.).

The inaugural Devon report was made at Plympton in 1861. Again, no further Pine Hawks were detected here until about a century later – at Rousden in 1960 and at Torquay in 1966 (McCormick, 2001). In Cornwall the moth has only been seen in an unspecified locality in 1908 (Curtis, 1930a), at Newquay in 1976 (B. N. Boothby; in Smith, 1984), and at Seaton in 1979 (R. Carter) and 1984 – latterly when several were noted (J. Ingram).

The Remaining Novel English Records

Alongside the serial histories just listed, occasional sightings of rogues or pioneers were also recorded. For example, reports came from Hitchin in Hertfordshire in 1844 (Foster, 1937), Deal in Kent in about 1875 (Tutt, 1904), Tunstall in Staffordshire in 1880 (Curtis, 1930b), in Herefordshire in 1881 (Battiscombe, 1881), at Salisbury in Wiltshire in 1895 (Gummer, 1895), at Winchester in 1902 (Goater, 1974) and in another unidentified spot in Hampshire in 1903 (Stevens, 1930), at St Anne's on Sea in Lancashire in 1907 (Curtis, 1930b), in West Sussex "in or about 1917", where one was "taken at rest on a pine trunk near West Burton" (Adkin, 1932), near Polegate in East Sussex in 1919, where a perfect fertile female was found "resting on a telegraph-pole near some pine trees" (Adkin, 1930), "from a tree-trunk" at Haslemere in Surrey in 1925 (Oldaker, 1926), and the species was also seen at Folkstone and Halling in Kent in about 1920, at Ham Street in the same county in 1930 (Chalmers-Hunt, 1960-81), and the sole Worcestershire sighting came in 1995 (P. Holmes).

The history of contiguous territorial change

There were four main geographical districts for *pinastri* available to avid early collectors – transiently early on in Scotland and near London, and later more permanently around Suffolk and in Dorset. Between the two world wars, sourced from the Dorset colonies, the Pine Hawk struck out northwards and eastwards in a great colonising thrust – the first Wiltshire record of the sequence was made at Salisbury in 1944 (Pitman, 1954) and that in Oxford in 1948 (Emmet, 1957). By the 1950s, a large area for the moth had been founded in south-west Norfolk, by 1955 it had penetrated as far north as Boston in Lincolnshire, and by 1976 to Thoresby in the same county (Duddington & Johnson, 1983) – although a temporary halt to its boreal adventure took place during the 1960s and early 1970s. During the late 1970s, the species was said to be "Almost entirely confined to Dorset, Hampshire, Surrey, Norfolk and Suffolk" (Gilchrist, 1979). However, its range was already far more extensive than that – for example, the insect was locally quite commonplace across the two Sussex vice-counties (Pratt, 1999) – as Figures 1 – 6 illustrate.

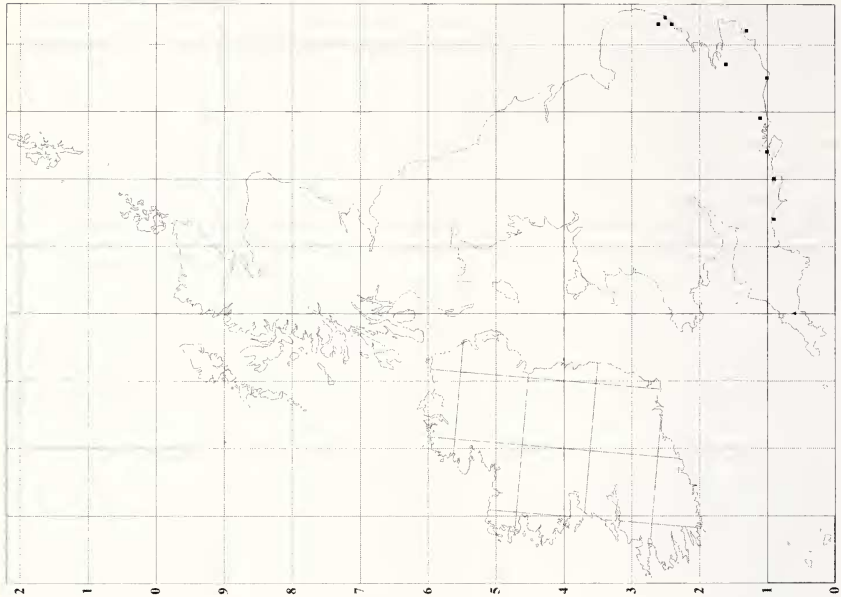

Fig. 2. *S. pinastri* – distribution 1908 to 1924.

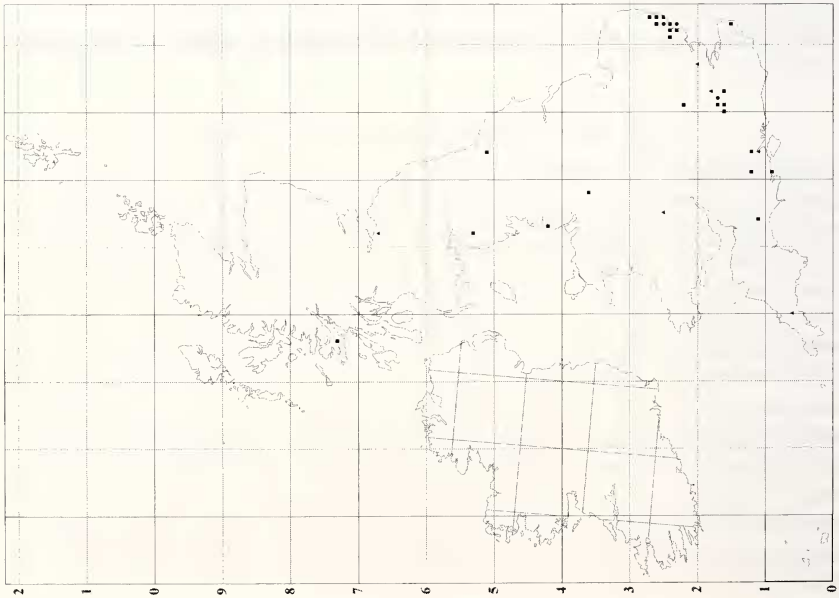

Fig. 1. *S. pinastri* – distribution up to 1907.

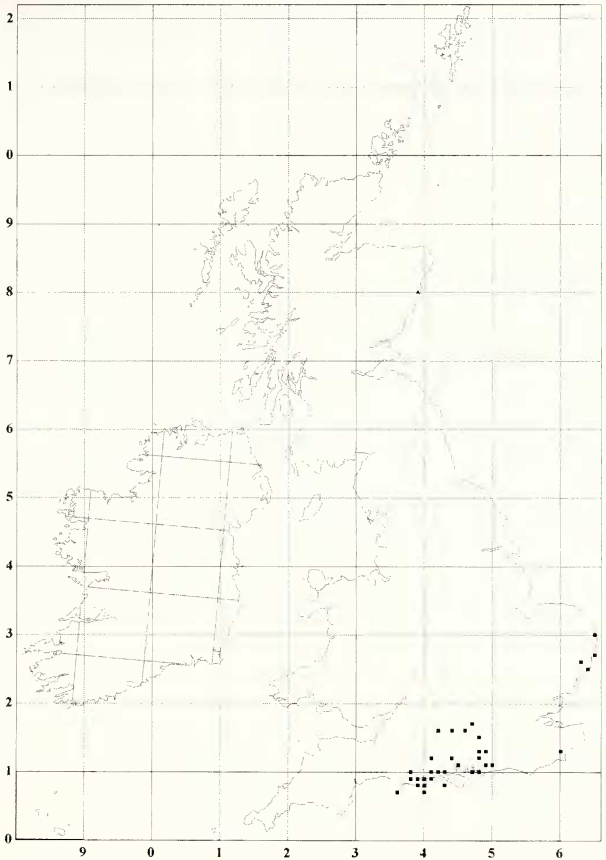

Fig. 3. *S. pinastri* – distribution 1925 to 1947.

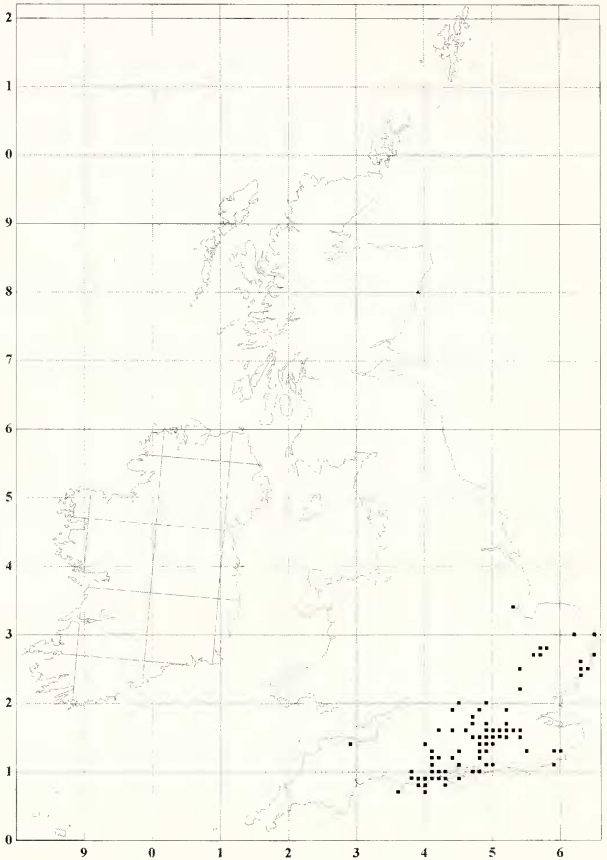

Fig. 4. *S. pinastri* – distribution 1925 to 1959.

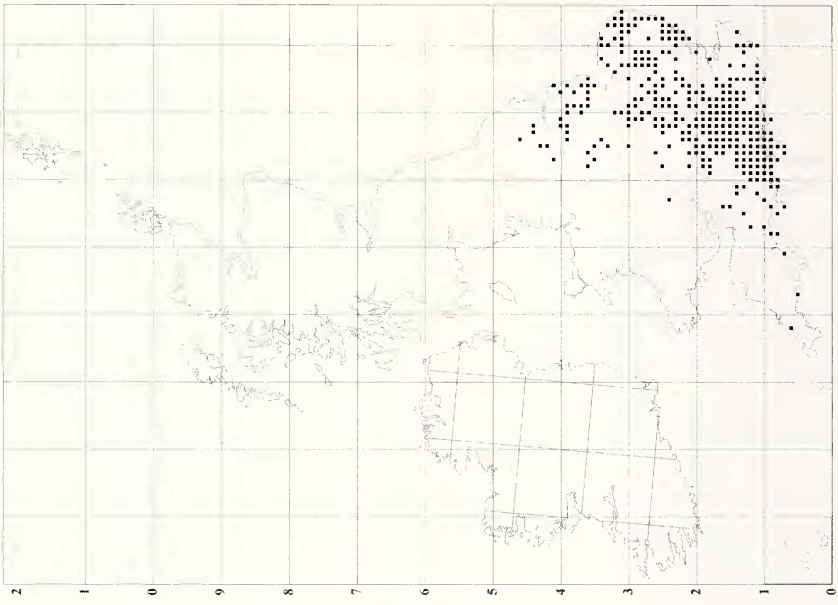

Fig. 6. *S. pinastri* – distribution 1960 to 2000.

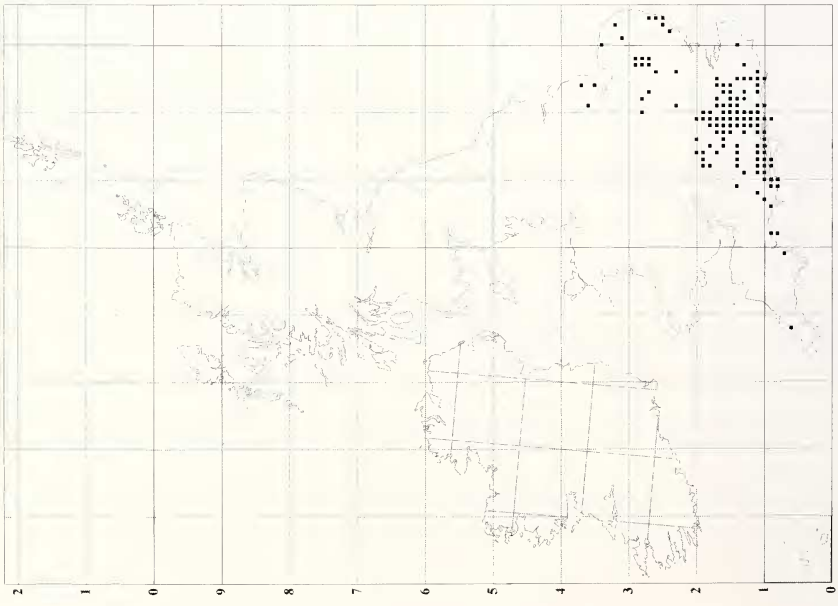

Fig. 5. *S. pinastri* – distribution 1960 to 1979.

The start of the expansion in range has always been dated to the 1930s (Allan, 1947: de Worms, 1962: Newman, 1965: Gilchrist, 1979), but there seems little doubt that it was under way a decade earlier. Bearing in mind that the adult stage's numerical potential is always established from June onwards during the previous season, 1929 was judged probably an "optimum" one for adults in Dorset (Curtis, 1930a) – and 1928 was numerically the most advantageous season for adult British macro-Lepidoptera for a decade (Beirne, 1947b). At a minimum, the insect's territory in that particular district was estimated to be encompassed by an 18-mile walk, which, if a theoretical circle, could mean the colony already covered around 25 square miles. During the same year the moth also suddenly appeared 10 to 15 miles to the north-east of its Dorset headquarters, at Picket Post in Hampshire, a county where collectors regularly took specimens from at least 1935 onwards (Goater, 1974). However, the very first sign of this sequence may well have been signalled by the Haslemere sighting of 1925, which would neatly fit in with the average speed and geographically directional events that took place over the next two decades. It is also known that "Ranges represent local response intensities to environmental variables" and often include "a response lag" before colonisation, even amongst flying organisms (Hengeveld, 1990: Ford, 1982). So it could also be speculated that the previous Hampshire records, in 1902, 1903, and 1917, indicate that there may have been even earlier tentative and episodic false starts to this spread, which ebbed and flowed to and from the north-east. Whatever, the moth finally swept across the whole of south-eastern England during the middle quarters of the century, during the second quarter at an average rate of between four and five miles per annum, which is a typical pace for such events. The northern-most serial native sightings within its continuous range are currently being made in the York district of Yorkshire.

The source of early colonies

Much discussion has publicly and privately taken place over the origin of the early British records. There are five logical alternatives for the source of the pioneering British records and colonies. (1) The moths had simply been misidentified, (2) were accidentally imported with pine seedlings or in a crevice on board a ship, (3) foreign specimens were deliberately released by dealers, (4) both permanent and transient colonies were founded by continental immigrants, or (5) the insect was long-native to each of its three main stations.

Misidentification

It has been said that "No moth could be mistaken for *pinastri*" (Allan, 1947), and many other early chroniclers completely dismissed misidentification as a source of error, as, to the eyes of experts, there were no likely *doppelgangers*. However this may have been to the experienced observer, the Convolvulus Hawk *Agrius convolvuli* has always been a potential contender for confusion amongst less experienced lepidopterists. Some of the earliest hand-painted illustrations depict similar-looking

moths (Harris, 1766: Westwood, 1854) and, even now, with easy access to peerless identification books of comparative photographs, such errors do still initially take place in regions where both moths are rarities (R. Leverton). So it is just possible that details of the odd *convolvuli* sighting did pollute the northern record of the Pine Hawk, although investigation shows that there is no bias towards good seasons for the arrivals of this migrant elsewhere in Britain. It may be thought that sightings made late in the year are especially likely to be of the Convolulus Hawk, as this is the time when by far the largest numbers arrive from the continent. However, in Sussex for example, native *pinastri* have been seen during every week of the year between late April and early September inclusive (Pratt, 1999), and in Hampshire there is even a late September record (Curtis, 1930a). It is also occasionally said that there could be confusion with some forms of the Privet Hawk *Sphinx ligustri* (Pittaway, 2000), which is another immigrant (Gilchrist, 1979: Skinner, 1984: Pratt, 1999; 2001). Still, there can be no doubt over the accurate identification of some of the Scottish records, as a surviving specimen from Dr Leach pinned in the Dale collection section of the Hope Entomological Collections housed in Oxford University Museum testifies – it is labelled "Rivelston Wood, near Edinburgh Mr Wilson 1818" (D. Mann).

Accidental Importation

The idea that the apparently rogue records of this moth were due to "stowaway on some trading ship" was put forward throughout the 20th century (Lofthouse, 1903: Newman, 1965: Sutton & Beaumont, 1989). Amongst almost all butterflies and moths, this is a now discredited explanation for what have been natural migrations from the continent. But, easy though it is to quickly dismiss this suggestion as old-fashioned and at most numerically inconsequential, it is an extraordinary and uncomfortable fact that the original east coast colonies of *pinastri* were clustered between the ports of Harwich and Lowestoft, those in Dorset near to Poole Harbour, the settlements at London were situated just to the south-east of the docks, and that at Edinburgh existed near ships tied up at Leith on the River Forth; even the Yorkshire singleton of 1900 was taken three miles from Tees Mouth docks.

Ships berthing at London have travelled the world for centuries. Napoleonic wars permitting, the wood and canvas sailing ships of the early 19th century and some of the great tea clippers of the 1840s traded with mainland Europe, just as by 1904 Harwich had regular steamship contacts with Denmark and Holland, and Edinburgh/Leith with Holland, southern Norway, and Hamburg in Germany (Bartholomew, 1904) where the Pine Hawk was sometimes "the commonest of the family" (Smith, 1955). But it is far more likely that any accidental introductions of *pinastri* were strictly associated with the importation of small evergreen trees, the chances of a series of completely casual imports being extremely remote. Experts first proposed this idea in 1886 and later authorities agreed that it remained "a possibility" (Jordan, 1931: Beirne, 1947a: Newman, 1965) – and the eccentric Cumberland record

from the 1820s was specifically listed from a "fir plantation". A survey of ancient pollen records carried out on the Isle of Mull in 1999 – where *pinastri* larvae were found during the early 1860s – concluded that there was no good evidence that pine trees had any antiquity on the island, and that any such 19th century woods were indeed artificial (R. Tipping). This confirms that the species could well have been unwittingly introduced here with pine seedlings. On the other hand, such occasional flukes should have also turned up in Wales and Ireland – but they have not.

While small-sized pines had probably been previously grown in this country on a small scale for decades, in the year of 1919 the freshly inaugurated Forestry Commission started the first continuous large-scale propagation of Scots Pine at their school for foresters set up at Parkend in Gloucestershire's Forest of Dean (G. Botwright). The fresh production of quantities of cheap home-grown seedlings would soon have replaced comparatively expensive ship-borne foreign imports. Nowadays there are at least 31 large nurseries producing these trees, scattered throughout the British Isles (N. Day, Forest Enterprise). After more than a century of the insect's sporadic history, amounting to seven geographically-bizarre records made north of an imaginary line drawn between the River Severn and the Wash, only one such *pinastri* sighting has come to notice since 1908 – a pair of freshly emerged adults found near Aberdeen in 1928, a port with ships then only substantively plying trade to London (Bartholomew, 1904: Philip, 1935).

Deliberate Importation

Some authorities suspected that the activities of nefarious insect specimen dealers were at the source of all early British records, adding that "This species appears to have no real *locus standi* in the British fauna" and that all of the 19th century Suffolk records were "the result of an attempt to acclimatise the species" (Tutt, 1904: Jordan, 1931). But merchants would not have had much commercial incentive to purposefully introduce the species to various places as far north as Scotland.before the middle of Queen Victoria's reign – while there was a small regular trade for natural history specimens by the early years of the 19th century, the infamous British barter market only really first rose to prominence during the mid 1850s, peaking around the 1890s. Just as today, while no doubt a few *pinastri* were sporadically and casually released by amateur breeders, too many different private collectors of good repute were intimately associated with the moth's early history, some with detailed sequential entomological diary entries, for there to have been an extended and deliberate ongoing fraud by professionals.

Migration

Across the Straits of Dover the European mainland is situated about 26 miles away from England. While not all modern authorities apparently accept the principle (Gilchrist, 1979), almost throughout entomological history, migrations from the continent have been tentatively suggested as a source of British *pinastri* specimens,

these ideas concerning either single vagrants or more determined episodic bids to colonise our islands (Tutt, 1902: Allan, 1947: Newman, c.1949: Chalmers-Hunt, 1960-81: Newman, 1965: Ford, 1967: Pratt, 1999; 2001). European experts on the mainland hold similar suspicions (Eitschberger, Reinhardt, & Steiniger, 1991). B. Beirne, the mid 20th century's national authority on the origin of British butterflies and moths, concluded in a classic paper (Beirne, 1947a), that *pinastri* could be one of those insects "which arrive by overseas migration and establish themselves for shorter or longer periods but eventually die out, to re-establish themselves at later dates", although he was unable to eliminate accidental importation as an alternative explanation in this particular case. There is no good evidence that the Pine Hawk has been permanently established in northern Britain since the early 1860s – but the intermittent series of encounters made between the late 18th century and that time, of both larvae and adults, does suggest temporary residencies similar in nature to those of other species which are now generally accepted to have been founded by continental colonisers during modern times. Such a migratory instinct could also indirectly account for the rogue event at Aberdeen in 1928.

Some good circumstantial evidence of migration from the continent has been provided from the south coast of England, from Sussex (Pratt, 1999) and perhaps "a sandbank facing Poole Harbour in Hampshire" (Turner, 1931). Best of all, on 1 June 1953 a single Pine Hawk was "seen flying N. against the wind" at the Royal Sovereign light vessel moored seven miles out to sea off Bexhill in the English Channel, where the moth was eventually identified after coming to rest on board (French, 1954). The national distribution map of *pinastri* from 1908 to 1924 is also typical for that of an occasional continental immigrant, with sightings just being made in almost every south-facing coastal county.

At least two European mainland Hawk moths have been expanding their ranges during recent times. For example, another pine-feeding species, *Sphinx morio* R. & J., has pushed northwards during the past 20 years, displacing *S. pinastri* in the process (Pittaway, 2000); and *Proserpinus proserpina* Pall. was freshly recorded in about half a dozen countries to the north of its normal range during the 1980's (loc. cit.), including here in Britain – to mv light in East Sussex in 1985 (Pratt, 1985; 1999) and at rest in East London in 1995 (Skinner & Parsons, 1998). There are further similar precedents amongst the butterflies. These include the European Map *Araschnia levana* L., which temporarily colonised Monmouthshire and Herefordshire around the years 1913/4 but was not seen here again until a single immigrant or vagrant appeared in Surrey in 1982, and which expanded its European range during the last half of the 20th century (Emmet & Heath, 1989); and, even more coincidentally, there was the brief unique establishment of the Queen of Spain Fritillary *Argynnis lathonia* L. on the Suffolk coast during the mid 1990's, a species which increased during the same decade in adjacent countries on the continent after earlier serious declines on some other areas (Wilson, 1998: Asher, et al., 2001).

In summary, the arrival of occasional migrations of *S. pinastri* from the continental mainland is a distinct probability.

Native colonies

Some leading authorities believe that the Pine Hawk has been indigenous to some parts of Britain for millennia, although E. A. Cockayne observed that "*Pinastri* can scarcely be regarded as native in the sense that many of our moths are, if it be true that the pines in the midland and southern parts of England were all destroyed" by the Ice Age, and that "the tree was replanted in comparatively modern times" (Cockayne, 1926). It is now known that, during some of the major Ice Ages, glaciers swept across much of the British Isles, although during the last, that of about 15,000 years ago, "most of central and southern Britain remained ice-free" (Stuart, 1988). Even so, it seems unlikely that *pinastri* could have survived such associated cold for long, even in the south. Cockayne (1926) believed that there was "little doubt that it introduced itself naturally", and that this took place after the last great freezing epoch.

Judging from a published geological map (Philip, 1935), all three of the conglomerations of English colonies which are thought to have existed before the 1920s – those near London, Dorset, and Suffolk – were exclusively situated on islands of well-draining "Tertiary Sands & Clays". Scots Pine has flourished on these sands for centuries – some say indigenously, for 10,000 years (Curtis, 1930), others that it is a long-naturalised "presumed introduction" away from northern Scotland (Perring & Walters, 1982: Phillips, 1978) – but the "naturally growing" trees have always been much less frequent away from this type of soil in England. As there were no breeding settlements of *pinastri* on other earths, this implies that all early colonies were first established before the time of the widespread introduction of artificial pine plantations – that is, prior to the 1820s and 1830s. As usual, the Pine Hawk's Scottish settlement is the exception, as Ravelston Wood is positioned on Boulder Clay (and Balerno on Carboniferous Sandstone) surrounded by highly complicated geology. But, supportively, the colony is known to have definitely been in existence here since at least around the 1790s and some believe that Scots Pine has been long-native "in a few places between Yorkshire and Sutherland" (Step, c.1910).

Colour forms

C. G. Barrett (1895) stated that the Pine Hawk was "not very variable" and that "English specimens are frequently plain in appearance" in their grey, grey brown, or "exceptionally brown" ground-colour. By the 1930s, later entomological authorities had noticed that several distinctly different colour types then existed in the British Isles. More importantly, the two main forms – grey and cream – were concentrated into two separate geographical areas. By the late 1970s, variation was being described as "confined to the intensity of the wing pattern", to black markings on a dark grey ground-colour, although "almost unicolorous brown" specimens were also being noted – much as had been chronicled by Barrett. However, no mention of cream-coloured moths was made (Gilchrist, 1979). While most experts have held that many centuries of natural selection

within restricted and isolated environments has resulted in divergent local colour forms, it could also be argued that two different races arrived in England from the continent.

From a number of observations made from 1922 to 1924 amongst both bred and wild-caught adult specimens originating from Saxmundham in Suffolk, two series of opposite colour forms were obtained. These concerned the extreme but locally commonplace "very pale whitish brown" or "cream" ab. *albescens* Cock., and the scarce "very black" ab. *unicolor* Tutt (Cockayne, 1926: illustrated in Turner, 1926; plate 9). In 1931, *unicolor* was still occurring as a great rarity in the wild (Nash, 1931) and nine years later there remained "a tendency amongst the Suffolk specimens... to a lighter and a more chalky ground colouration of the wings and body than those specimens from Dorset" (White, 1940). However, one of the foremost current Suffolk moth recorders, J. Nicholls, states that of around 35 moths examined at Ipswich in 1998, almost all had the usual "grey ground-colour", that there was "only one, or possibly two, of the brown variety", and that no black or cream examples were detected (pers. comm.).

Throughout its history here, similar contentions have been made about Suffolk larvae – the Pine Hawk's caterpillars also enjoyed a long-held reputation for being unusually variable. Larvae were basically dimorphic, exhibiting a green or brown ground-colour, although there were also many intermediate forms (Tutt, 1904). Caterpillars painted from Leipzig stock of 1882 picture a green form with a broad brown dorsal stripe (Buckler, 1887).Compared to German examples, 19th century Suffolk larvae were considered "much less bright in colour, the dorsal region broadly light brown, with darker brown clouds on each segment, and the sides mixed brown and greenish or yellowish" (Barrett, 1895). Other Victorian collectors found our English examples were "of a bright green ground-colour or in some cases of a reddish tinge" (Lucas, 1895). Seventy years later, after extensive experience breeding the species, L. Hugh Newman confirmed that larval colouration differed according to the country of origin, stating that "The fact that larvae of Suffolk stock tend to be more sombre in colouring in the final skin than the progeny of pupae imported from Germany, seems to indicate that they are a somewhat local form which may have been isolated for a long time" (Newman, 1965). An illustration of a West Sussex caterpillar bred at some time during the final quarter of the 20th century depicts a bright well-contrasted "reddish-brown" form, "heavily marked with white and dark brown on the back and sides and dark green also on the sides" (Porter, 1997).

Meanwhile, during the second quarter of the 20th century in the south-west of England the adult population was mainly composed of "slaty-grey" moths (Jeffreys & Birkett, 1941) or "grey-brown forms" (Turner, 1936), there being "a tendency of the average Dorset specimens towards darker and browner markings than those of Suffolk" (White, 1940). Evidently a single melanic was also seen in Dorset (Kettlewell, 1973). In the same county at the same time, "red-brown" examples also occurred as a small percentage of the feral population at Wareham (Jeffreys & Birkett, 1941). But in Sussex, situated 40 miles away to the east, there have never been any

reports of black, whitish, or red-brown *pinastri*. Throughout its permanent establishment here, since 1942, colour variation amongst the typically grey adults has been "Usually slight... although the darker markings do vary in intensity", these specimens being as illustrated in Skinner, 1984; pl. 19, fig. 10 (Pratt, 1999). Judging from the colour of the Edinburgh specimen of 1818, the curious Scottish colony was also composed of grey moths.

In 1904, Tutt pointed out that internationally "There was a very wide range of variation in this species", including ground-colours ranging from whitish, grey, and brown. He confirmed that, while "The more common central European form is of (a) slaty-grey hue", two "magnificent pale" specimens "with greyish-white forewings and deep brown characteristic lineolae", existed in London's Natural History Museum. These were labelled "Berlin", although a footnote frustratingly added "it is quite possible" that these insects "were not captured in the Berlin district" (Tutt, 1904). Still, it seems that a whitish form of the Pine Hawk with brown markings then occurred in Germany. However, by the 1960s a melanic form dominated in some parts of the Netherlands (U. Eitschberger) and in industrial areas of Czechoslovakia (Kettlewell, 1973), and within a decade the black *nigrescens* Lemp. (indistinguishable in colour from ab. *unicolor* Tutt) had "in a comparatively short time (become) dispersed over the whole country" of Holland (Kettlewell, 1973). Nowadays the moth remains "very variable" on the continental mainland, a recent assessment stating that "The normal grey colour may be of almost any shade", "ranging from dark brown (f. *brunnea* Spuler) to cream (f. *albescens* Cockayne)" (Pittaway, 2000).

The first records of melanism within Suffolk Peppered Moth, *Biston betularia* L., were made in 1895 (possibly 1894) (Kettlewell, 1973) and in 1898, both at Ipswich. By the mid 1930s, it was being said that the black form, f. *carbonaria*, "used to be rare... but is rapidly spreading to our rural districts" (Morley, 1937). By the 1950s , perhaps surprisingly, fully three-quarters of the Lowestoft population were black, and during the following decade two-thirds of those at Sudbury (Kettlewell, 1973). Since that era the form has greatly diminished country-wide. The history of melanism within *betularia* apparently proves that the local environment became increasingly darker during the 1930s and 1940s, peaking during the 1950s and 1960s. Just how relevant these high levels of black Peppered moths are, so far as grey or cream forms of the Pine Hawk are concerned, especially as there was no increase in its own black ab. *unicolor*, is speculative.

In the absence of any evidence of a permanent significant alteration in the Suffolk environment towards a grey landscape, and in the presence of a wave of such-coloured colonising *pinastri* from the south, the stark quantitative change in the comparative adult colour forms found in the county between the second and final quarters of the 20th century – from cream, to grey and sometimes brown – suggests that the early predominantly light form was completely overwhelmed by the later invading grey Dorset race. If long-acting natural selection in Suffolk had dictated a light-coloured moth, the darker colonising race should have become unsuccessful in the area, with the colour of survivors becoming attenuated towards the paler form.

While the change to grey forewings was indicative of an environmentally different race, colour was not the driving force behind colonisation.

The causes of territorial increase

Perhaps the most important and remarkable part of this insect's history is that, after more than a century of episodic and severely localised existence on our island, specimens from Dorset suddenly proceeded to colonise more eastern counties. Nevertheless, even after around three-quarters of a century of subsequent expansive effort (with a brief break during the 1960s and early 1970s), the insect has been unable to properly colonise adjacent areas situated in the west of Britain; even along the south coast, permanent settlements still peter out in Dorset.

A lowering of the numerical levels of the Pine Hawk in the wild has been attributed to a number of different factors. There has been notional death from insecticide spraying at Cannock Chase (Allen, 1955) and over-collecting at Bournemouth (Postans, 1948), more definite losses due to infertility, frost (Cockayne, 1926), and the parasites *Phryxe vulgaris* Fall. and *Protichneumon pisorius* L. in Suffolk, Norfolk, and Hampshire (Styles, 1958), and breeders have also encountered attacks by viruses (Porter, 1997) – but no convincing idea has so far been advanced in explanation of the great increase in English range.

The Increase in Pine Plantations

The enlargement in territory that the Pine Hawk enjoyed during the 20th century is often simply and directly attributed to "the increased planting of conifers" (Gilchrist, 1979: Pittaway, 1993; 2000) that took place after the formation of the Forestry Commission in 1919. Ever since that date the Commission has been inserting evergreen trees in large plantations across the country, especially in the north. Naturally, pines have been preferentially introduced to habitats which produce the best quality timber and the fastest grow-rates – that is, in dry and sandy soils – although the Lodgepole Pine comes to the fore in northern Britain due to its superior toleration of the generally more exposed and damp conditions (N. Day, Forest Enterprise). During the 1920s, away from the far north, the English home of foreign pine was in the counties of Hampshire, Berkshire, Surrey, and Gloucestershire, as illustrated in figure 7. Similarly, by the end of the century the tree's headquarters were situated in coastal counties from East Sussex to Dorset, and Norfolk and Suffolk, while inland Worcestershire, Nottinghamshire, and South Yorkshire were just as prominent – but Surrey and Berkshire had become the counties most densely populated with these plantations, as illustrated in figure 8. Similar levels exist in Ireland – 69,000 hectares of pine are currently growing on the island, this amounting to about one percent of the total land area (M. Twomey & G. Cahalane, Forest Service) – yet this is a land where the Pine Hawk has so far gone completely undetected.

Despite currently holding an unprecedented amount of territory, the distribution of modern *pinastri* colonies has been restricted to England where presently almost 130,000 hectares of conifer trees exist. Pines are now the second most numerous national tree after the oak (Forestry Commission, 2001). But it is rarely appreciated

that such plantations have been substantially increasing for more than 170 years and, most importantly of all, that more than 60% of today's area of pine was already in place before the moth's colonisation got well under way. While Scots pine has been here since after the last serious Ice Age, the first of a series of related foreign trees, the Corsican pine, was originally introduced in 1792 – and this is a species which currently accounts for a third of our pine acreage.

It is known that there was at least one fir plantation in Cumberland by the late 1820s (Marshall, 1842). During the 1830s the practice grew apace elsewhere, with the arrival of a number of other evergreen species (Mitchell, 1981: Grimes & Herbert, 1988), and by 1924 79,000 hectares of pine plantations were already being cropped in England (Forestry Commission, 1928) (figure 7). While the proliferation of artificial sympathetic habitats has doubtless been the most significant factor in the insect's modern high density of distribution, all of the detailed evidence and distinctive history assembled here shows that the insertion of 411,000 hectares of alien pine trees on the British mainland made no material contribution to the change in range.

There are only a few records of *pinastri* larvae feeding on spruce, although the tree is sometimes spoken of in the same terms as pine as a foodplant (Gilchrist, 1979). An examination of the distribution maps for spruce, figures 9 and 10, shows no correlation at all with that of the territory held by this moth, so it can be safely stated that this particular tree has certainly played no significant part in the British history of this insect.

Climate

It is known that "species ranges can be considered as optimum-response surfaces with a complex internal structure" and that they are "dynamic entities over the long or short time scales and can be considered as outcomes of a process of perpetual adaptation to changeable conditions": "Climatic conditions may be of prime importance to the probability of establishment and eventual success of invading species", and why most invasions fail (Hengeveld, 1990). In 1930, W. Parkinson Curtis listed this insect as one of those "resident species which find our climate trying, and have a struggle to maintain a footing, but are successful in doing so" (Curtis, 1930a). Just which components of our weather were considered detrimental was not mentioned, although frost has been known to kill larvae. For example, in Suffolk in 1922, probably before the main expansion in range, it was said that "Infertility coupled with the lateness of the larvae and their susceptibility to frost perhaps accounts for the relative scarcity of *pinastri* and its inability to spread in this country"; on a large sample of "hundreds" of eggs obtained from several different Suffolk females, an infertility rate of around 50% was recorded (Cockayne, 1926). However, the early history of the Pine Hawk's colonial presence – albeit perhaps temporary – in comparatively cold Scotland, its long-term absence from the warm extreme south-west of England, and its European distribution (discussed later), disputes the idea that frost is a serious depressant force on numbers and overall range; the fact or effects of any abnormally-high levels of infertility within the general feral population of *pinastri* since the 1920s have yet to be reported.

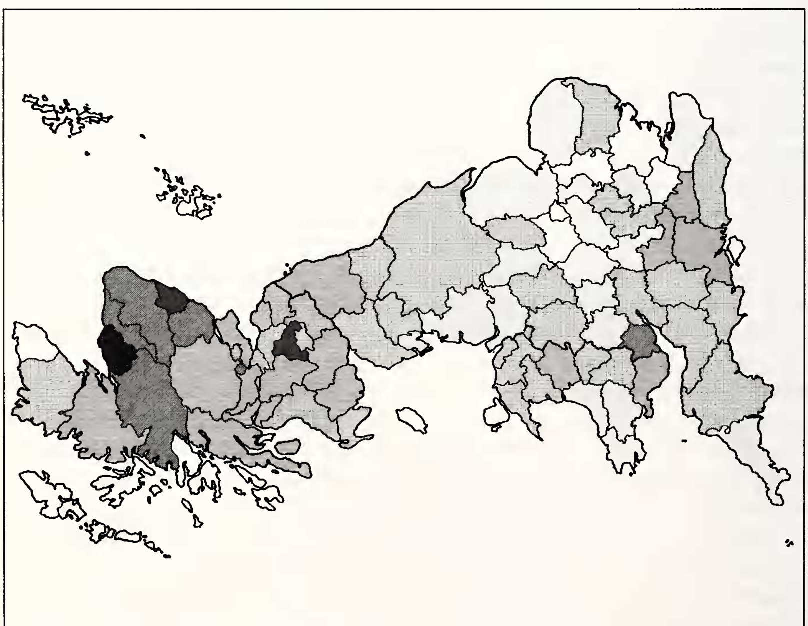

Fig. 7. The Density and Distribution of Pine Plantations in the Counties of England, Wales and Scotland, in 1924

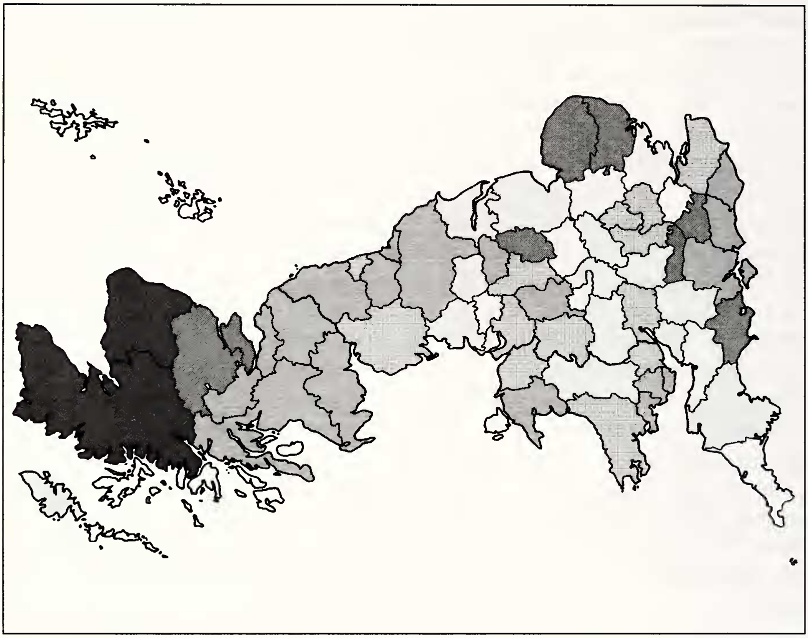

Fig. 8. The Density and Distribution of Pine Plantations in the Counties of England, Wales and Scotland, from 1994 to 1999

Fig. 9. The Density and Distribution of Sitka Spruce Plantations in the Counties of England, Wales and Scotland, from 1994 to 1999

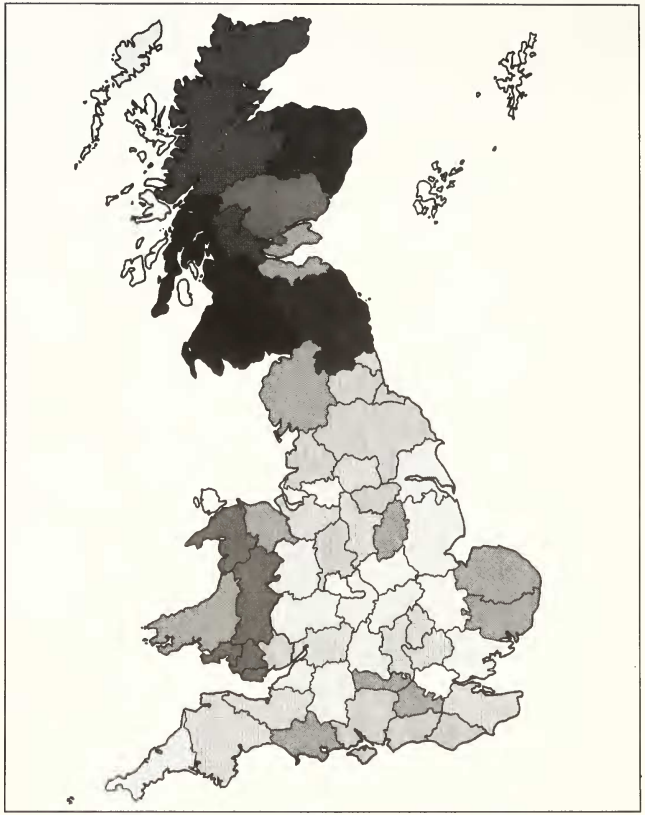

Fig. 10. The Density and Distribution of Pine and Sitka Spruce Plantations in the Counties of England, Wales and Scotland, from 1994 to 1999

The moth's national distribution is surprising similar to that of the Stag Beetle *Lucanus cervus* L., as recently illustrated (Napier, 1999: P. T. E. S., 1999). It is now known that large parts of this beetle's local range are intimately determined by long-term rainfall, high levels being geographically deleterious (Pratt, 2000). In addition, it was observed many years ago that "a succession of seasons of gradually increasing rainfall is detrimental to Lepidoptera" (Beirne, 1947b). Not surprisingly, the Moth Recorder for Devon, R. McCormick, considers it "very odd" that *pinastri* can be found at Wareham in adjacent Dorset but not in his home county. McCormick confirms that there is currently "no lack of foodplant", and shrewdly suggests that Devon "must be too wet" (pers. comm.). On the other hand, where the Pine Hawk's colonies finally peter out in Dorset the soil where successful pupation takes place "is most usually sandy peat, which is frequently very wet", and occasionally "submerged some inches up the trunk with flood water" (White, 1940). Still, breeders have noticed that Pine Hawk pupae "dry out easily" (Friedrich, 1986).

The geographical distribution of annual British rainfall exceeding 100 centimetres (Fig. 11), has remained reasonably constant during the 20th century (Philip, 1935; 1996: Meteorological Office, 1999). Perhaps surprisingly, the wet autumn and winter of 2000/2001 notwithstanding, there is no evidence that varying long-term rainfall (Nicholas & Glasspoole, 1932: Central Statistical Office, 1933 et seq.) – either during a full length of the insect's life-cycle, during July when ova are at their peak, during August and September when larvae are feeding, from October to May when pupae are underground, nor from June to July when adults are in flight – has any coincidence in timing with a territorially fluctuating *pinastri*. But, while there is no sign of an alteration in the quantity of rainfall being the driving force behind the insect's changing range, it is still true to say that a comparison of the geographical distribution of high precipitation in Britain and the insect's modern distribution prove that this *Sphinx* has so far been unable to colonise wet districts. Throughout both the UK and the continent, *S. pinastri* shuns the more humid westerly coasts; and, on the mainland, none of the pine-feeding Hawk moth species were recorded in western littoral districts during the 20th century, including those facing the Mediterranean and Adriatic Seas.

"The relative humidity of the atmosphere and the effectiveness of most precipitation are directly affected by prevailing temperatures". Moreover, "Temperature is probably the most significant climatic factor in biological terms as all metabolic processes (indeed most chemical reactions) are temperature-dependant" and"the annual cycle of temperature is perhaps of greatest significance in considering the biological impact of climate and climatic change" (Ford, 1982). Many associations have recently been made between high temperatures and the local territorial increase within individual butterflies and moths, and in the changing status of the Stag Beetle. It was concluded that "the disproportionate responses within these coincidences show that it is a change from an established norm of sometimes only a few years duration that causes modifications in range, and not necessarily absolute temperature values" (Pratt, 1999; 2000; in prep.). The Pine Hawk's pattern of

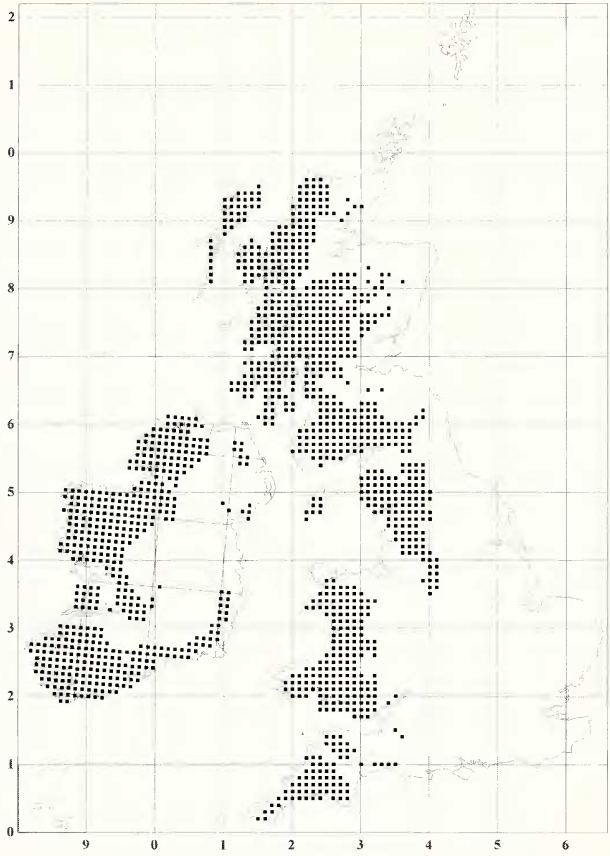

Fig. 11. Average annual British rainfall exceeding 100cms c.1961 to 1900.

colonisation also has some strong correlations with that of increased temperature. By the Second World War, meteorological researchers had gathered "very decided evidence of climatic amelioration round the North Atlantic since 1925" (Manley, 1944), although it was 1933 before really unfamiliar levels were attained in central areas of England (Manley, 1974). This eight year-long discrepancy may have been locally made up in our south-coast counties, as some districts – such as Dorset – are known to have been warmer at about that time (Philip, 1935) and since (Chandler & Gregory, 1976: Philip, 1996). "As climatic changes bring about a re-alignment of the location of the limiting isotherms (or isopleths – lines of equal rainfall – as the case may be) the distributional limits of organisms are correspondingly adjusted" (Ford, 1982). In 1956 Baron C. de Worms pointed out that "During the past twenty five years there appears to have been a distinct northward movement of a number of species of

Lepidoptera, chiefly moths whose normal habitat is in the more southerly regions of Europe". He added that there was "a definite movement to extend their range towards the north by some insects whose range just reaches the English Channel or the North Sea and by others of a more southern distribution". This afforded "ample evidence in support of the theory that this apparent movement towards the north of Lepidoptera and other creatures is most probably associated with the warming up of the climate in these more northerly latitudes of Europe, especially as some of the species of Lepidoptera are of distinctly Mediterranean origin and habitat" (de Worms, 1956; 1963). Now, more than forty years later, not only can it be confirmed that these phenomena have continued episodically and even accelerated to new heights (Central Statistical Office, 1933 et seq.: Manley, 1974: Jones, Wigley, & Wright, 1986), as illustrated in figure 12, but that the climatic change has also been named – natural "global warming".

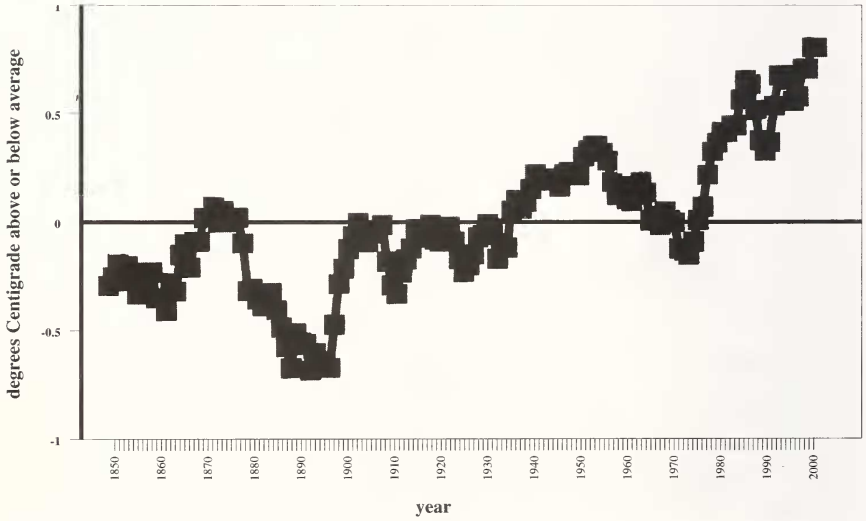

Fig. 12. A ten year running average of the annual temperature of England and Wales, 1850 to 1998.Calculated using the long-term average (1659 to 1998) of 9.40 degrees Centigrade, obtained from base data in Central Statistical Office, 1933 et seq.; Manley, 1974; and Whitaker, 1994 et seq.

It has already been proposed here that the birth of the Pine Hawk's extension in range is dated to 1925 or 1928, all previous authorities agreeing that it was under way during the 1930s. During a 200 year-long history, the timing precisely coincides with the start of the long-term increase in the hemisphere's annual temperature. The only significant sequential reversals in the 10-year average temperature trend in England and Wales since that time took place from 1950 to 1956, from 1962 to 1974, and from 1985 to 1987, inclusive (Manley, 1974: Central Statistical Office, 1933 et seq.). All of these periods coincide with an arrest in the insect's territorial ambitions in this m

country. For example, at the northern-most extremity of its range during the third quarter of the 20th century, the moth went completely undetected in the whole of Lincolnshire between 1956 and 1975 inclusive, since when it has been regularly seen (R. Johnson). Similarly, after being noted at South Thoresby in the same county in 1976, it was 1992 before the species had penetrated another 25 miles further north to Spurn Head to make the first of a series of Yorkshire records (P. Q. Winter). These coincidences strongly suggest that above average annual temperatures either stimulated a fresh race of continental *pinastri* to cross the English Channel and invade Dorset, or provided a more advantageous climate for a long-established "native" foothold previously naturally held in check. In an attempt to determine the stage of development in which the majority of Pine Hawk losses take place, graphs of July temperature (ova), August and September (larva), October to May (pupa), and from June to July (adult), were drawn up from base data (Manley, 1974: Central Statistical Office, 1933 et seq.) and again compared with the moth's territorial history, but all have serious irreconcilable anomalies.

A European perspective

During the 19th century Scots Pine *Pinus sylvestris* was described as "the typical Pine-tree of Northern Europe, where (especially in Russia and Northern Germany) it constitutes huge forests". Here it was "said to cover far wider tracts of country than any other forest tree" (Step, c.1910). However, the Hawk moth's 20th century boundaries only show a very loose agreement with the predominantly naturally-coniferous regions as illustrated in 1935 (Philip, 1935) and 1978 (Fitter, 1978). Its very early range in Spain and western France is even less sympathetic, although here the record of *S. pinastri* may well have been unwittingly contaminated with those of *S. moraurum* and, during both centuries, further more northern incompatibilities could be explained by migrations. Whatever, the early localities of the Pine Hawk on the European mainland were admirably and comprehensively determined by Tutt, when he listed all known sites (with limited dating) at the beginning of the 20th century (Tutt, 1904). The distribution map (Fig. 13) has been created here from Tutt's collation of more than 200 localities, together with a recently published map, (Fig. 14), compiled of more modern records (Danner, Eitschberger, & Surholt, 1998) for comparison.

The Pine Hawk moth's habitat has recently been described as being "open or mixed pine forests, especially... dry heaths; also in mountain conifer forests up to 1600m in the Alps" (Pittaway, 2000). Several 19th century authorities stated that *S. pinastri* larvae were "very abundant" and "sometimes very destructive to pine-forests on the Continent" (Meyrick, 1895). This was especially so in Central Europe (Kirby, 1897), but apparently not early on in Austria as the moth went unmentioned in "A Treatise on Insects Injurious to Gardeners, Foresters, & Farmers" (Kollar, 1840). One such event took place at Brandreis in Germany in 1827, when caterpillars swarmed "in such numbers that, in certain firwoods, the trees were completely stripped, and the pupae were so abundant in the autumn that they were used for feeding swine" (Tutt, 1904). Unusually high levels of larvae still sometimes occur (Gninenko, 1998), even

though "Wild larvae are often parasitised by ichneumons and flies" (Friedrich, 1986) – and more than two dozen parasitoid species have recently been identified (Pittaway, 2000).

Tutt observed that adults occurred "abundantly in many localities", although this may have been mainly restricted to "young plantations" – the species only flew "somewhat sparingly in most of the old pine forests... as well as in pine thickets that have long been isolated". In the Hartz mountains in Germany the insect also inhabited "the moor districts, probably spreading there from the lower forest region", while in Switzerland and the Albarracin district in Spain *S. pinastri* was established "for some distance up the mountains... to an elevation of a least 5000ft" (about 1,500m) (Tutt, 1904). Evidently the species was well distributed in France during the 19th century, where it was "very common, (in) woods round Paris" and "common" at Roumore and Nohant; in Germany it was commonplace in many areas and "very common" in the Rhine Palatinate; and it occurred "throughout" Belgium, Austria, and Czechoslovakia. The European record also proves that the moth could sometimes occur both in the comparatively dry and bitter cold of the Arctic Circle – under far more extreme conditions than were ever endured in Scotland – and in the heat of countries bordering the Mediterranean Sea. The extremities of its range then extended from woods in northern-most parts of Spain and Italy to Lapland, and at least as far east as Moscow and the Ural Mountains (Tutt, 1904). Even though the genetics of "European forms of a given species can tolerate a greater range of climatic extremes, particularly temperature", when compared to strains in the UK (Ford, 1982), whether the moth ever successfully bred in the coldest extremes seems unlikely. The species has also been unable to permanently colonise the hottest areas of Europe, including Portugal, most of Spain and the Italian peninsula, although there has apparently been an isolated record from Greece. The British records made in the south and east are in accord with this distribution, but those in the west and to the north of the River Severn are curiously discontinuous.

In 1931, K. Jordan divided the European Pine Hawk-moths into four subspecies, *Hyloicus (Sphinx) pinastri pinastri*, *H. p. medialis*, *H. p. maurorum*, and *H. p. cenisius* (Jordan, 1931), and almost half a century later another was proposed, *Sphinx p. euxinus* (Derzhavets, 1979). The subject is still under debate, three of the suggestions having recently been both authoritatively synonymised with the nominate race (Pittaway, 1993; 2000) and kept separate (Danner, Eitschberger, & Surholt, 1998). Whatever, *maurorum* is now acknowledged a distinct species by all, its distribution apparently being restricted to southern France (the northern-most record known was towards mid-France at Chateauroux, August 2002, by C.W. Plant), the eastern half of the Iberian Peninsula, and the north coast of Africa (Danner, Eitschberger, & Surholt, 1998: Pittaway, 2000). But all of these moths are generally so similar in appearance that the races, subspecies, and full species, can only be separated from straightforward *S. pinastri pinastri* by an examination of their genitalia (Jordan, 1931: Pittaway, 2000) – and these have been well illustrated (Jordan, 1931: Danner, Eitschberger, & Surholt, 1998) – and appear to breed and successfully hybridise together (including *S. maurorum*) (Pittaway, 2000). Whether or not Iberian-sourced *S. maurorum* have ever

occurred in the British Isles is therefore unknown, as every one of these insects would have been identified as the Pine Hawk by 19th century entomologists. To ensure compatibility, all are therefore embraced in the following distribution maps.

A comparison of the range held by pine-feeding Hawk-moths on the continent during early times with that of recent years shows an apparent retreat from south-western France and a concurrent colonisation of Denmark and Poland. This shift in European territory towards the north and east may have been concurrent with that in the same direction in England, but dated data is lacking. It has also been pointed out that *S. maurorum* has apparently displaced *pinastri* "in many southern areas" of France "over the last 20 years" (Pittaway, 2000).

Conclusion

There seems to be a combination of reasons for the complicated eccentricities of the early history of the Pine Hawk in Great Britain. The most likely true interpretation of the known facts is that the species has been an episodic immigrant from the continent for at least 200 years, and that this trait was the source of many of our early records and colonies. Just how much accidental importation played in this scenario is uncertain – it is impossible to logically differentiate between some records of immigrants and pioneering natives, their descendants, or chance conveyances and their offspring – but it is also impossible to dismiss the high coincidence between the geographical location of shipping ports and early *pinastri* records.

Judging strictly from the entomological record, the moth was intermittently resident in Scotland from the late 18th century until at least 1861, just possibly to 1928. Elsewhere, in Suffolk the species has been permanently established since at least 1872, possibly from before 1832, and near London from 1884 to 1907. Settlements in the eastern Dorset area have probably been in existence since at least the 1900s, possibly since the outlying southern Somerset sighting of 1853. However, the evidence provided by the exclusive presence of all three conglomerations of English colonies to Tertiary sand implies longer residencies, back to before the second quarter of the 19th century.

There can only be two possibilities that satisfactorily explain the increase in range since the 1920s. During this decade either the insect and/or the environment changed – either a new better-adapted race evolved in Dorset or freshly arrived from the continent, or the country's environment altered to become less detrimental to a race previously naturally held in severe check – enabling the species to overrun traditional settlements and eventually colonise much of eastern England. The precise coincidence of the Pine Hawk's hesitant territorial history with episodic rising temperatures during the 20th century prove that it was climate that has fundamentally dictated events, this perhaps explaining a parallel story on the continent. Distribution maps which illustrate the sequence of dated *pinastri* records between the 1920s and 1950s also show that the colonisation of England exclusively emanated from south-eastern Dorset. During the entire length of that climatically advantageous forty year period, this country's longest-known permanent settlements in Suffolk made no new concurrent expansion in range whatever – and this confirms that the insect's two early

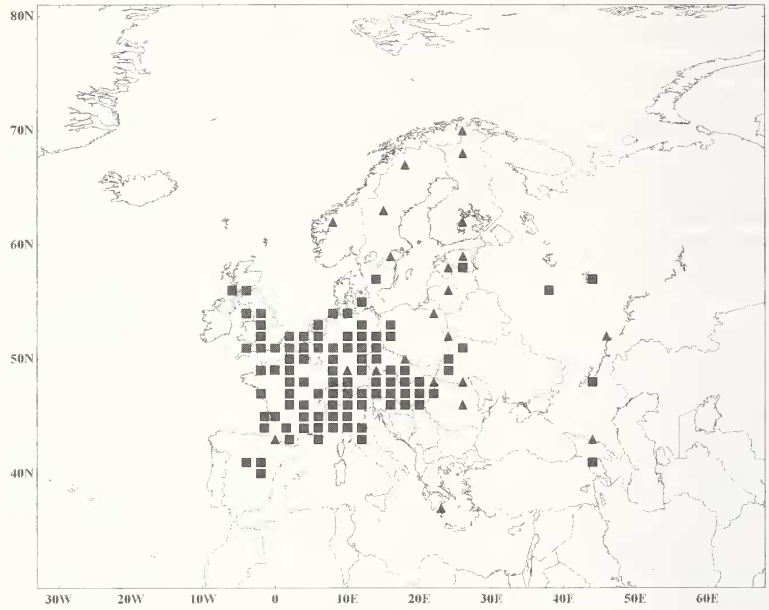

Fig. 13. The distribution of *S. pinastri* and *S. maurorum* in Europe, up to 1907.

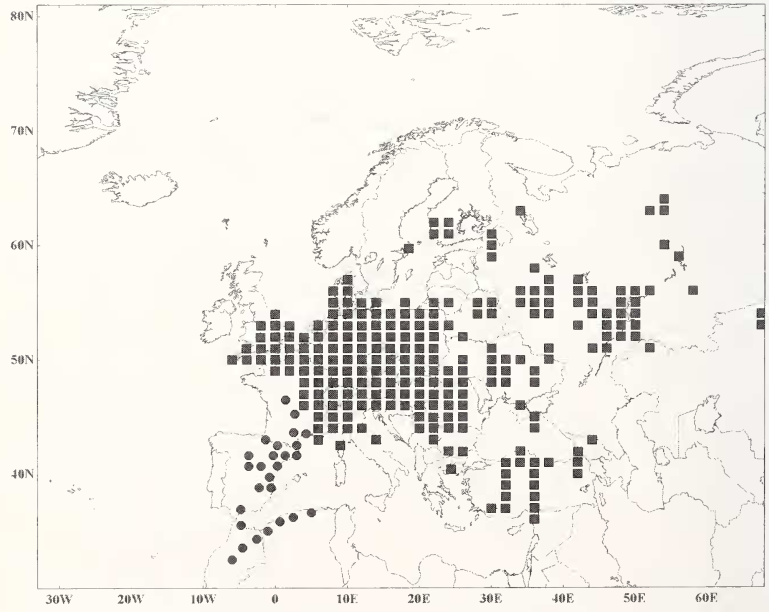

Fig. 14. The distribution of *S. pinastri* and *S. maurorum* in Europe, 1908 to 2002.

20th century headquarters were indeed composed of different races, the most southerly of which was, or became, better tailored to colonise England when rising temperatures came into effect. This judgement is also supported by the territorial history of the species colour forms. Whether or not the failure of the Suffolk colonies to extend their range was due to genetic differences which impinged upon their capacity to thrive under the same new climatic regime as our other main establishments, or to straightforward inbreeding (suggested by the low fertility rate and higher than usual levels of abnormal pale colour forms), has yet to be determined.

The future

While the intimate truth about all of the 19th century British records may now never be known for certain, recent scientific advances in the identification and matching of gene sequences could yet reveal much more about the origin of this insect's settlements. And, despite apparent compatibility within photographic illustrations of the genitalia of modern continental *S. pinastri pinastri* (Danner, Eitschberger, & Surholt, 1998) with some of those drawn prior to 1938 from Great Britain (Pierce & Beirne, 1975), the whole of this splendid insect's history entreats further such microscopic research into our Pine Hawk-moths, including comparisons of historic specimens from Scotland, Suffolk, and elsewhere, with those found in our current population and on the European mainland. With regard to future fieldwork, a comparison of modern-day Suffolk larvae with Victorian descriptions should confirm that a change to a brighter colouration has taken place – and an intensive investigative hunt for adults in its old Scottish haunts could still produce a surprise.

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Generic Names of Scarabaeoidea (Col.): a postscript

David Atty has furnished me with cogent data regarding the origin of the name *Aphodius*, which I had over-hastily treated in my recent notes as one of the more obscure names from the semantic standpoint – though its formation is clear. He shows that it evidently refers to a departure from the road or path (apo, hodos), probably for the purpose of obeying a call of nature, and cites cognate words in *Aristophanes, Aristotle* and *Plato*. I thank Mr Atty for illuminating the matter by the light of his scholarship.– A. A. Allen, 49 Montcalm Road, London SE7 8QG.